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Evidence of a random ovipositional strategy by female fruit fly *Bactrocera dorsalis* (Tephritidae: Diptera) with reference to host quantum

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Mango (*Mangifera indica* L.) is a favoured host of the fruit fly, *Bactrocera dorsalis* (Hendel), on which the females oviposit. Detailed laboratory studies were carried out to study the role of host biomass (= weight) on the oviposition decision of the tephritid fruit fly, *B. dorsalis*. The hypothesis that the biomass of mango fruit influences the decision of the mother (= gravid) fruit fly was tested on three varieties, *Alphonso*, *Totapuri* and *Banganpalli*, in three different but identical experiments. The results clearly showed that the number of oviposition punctures by a female fruit fly did not show significant differences among the different weight groups within a variety. The correlation coefficients between fruit weight and number of oviposition punctures were also not significant, i.e. the weight of the fruit did not influence the number of ovipositional punctures by the female fruit flies. This was true in all the three varieties. Further, the fruit weight did not influence the number of pupae that metamorphosed, number of adults that emerged and sex ratio in all the three experiments. The implications of these results on oviposition selection strategy of the female fruit fly are discussed. The study clearly indicated that after selecting a host (mango) the female fruit fly does not show non-random selection for a mango fruit with more quantum of pulp, as is expected if it were to maximize its survival and fitness.

Keywords: *Bactrocera dorsalis*, host biomass, mango, oviposition strategy.

AN organism exploits its resources to maximize its fitness. This is also true in the case of frugivorous insects. An insect, like a true fruit fly (Tephritidae: Diptera) ensures its fitness by favouring development of maximum number of progenies, through appropriating optimally the available food resource. The present study is on the tephritid, *Bactrocera dorsalis* (Hendel), a fruit fly that develops in mango (*Mangifera indica*) fruits. Earlier studies have found that food resource affects the development of the flies, as evident from differential pupal weights; poor food hosts result in lower pupal weight[1]. A fly would in all probability exploit its available food resources in such a manner that all its progenies have equal chance of survival. So, one would expect a fly to appropriate the pattern of egg-laying (oviposition) on a fruit depending on the quantum of a given food that would be available to its offspring, which would offset intraspecific competition. In the present context of the fruit fly, *B. dorsalis*, the adult female is expected to choose a mango fruit that can provide optimum quantum of food (fruit pulp) for maximum development of the maggots (the apodus pulp-feeding stage of a fruit fly) and ensure successful adult eclosion to the next generation. Thus all the maggots which hatch from the eggs are expected to have sufficient food for development into puparia, and metamorphose to fertile adults, ensuring a fit population in the next generation. If the food is inadequate, the maggots which manage to get sufficient food become fitter than the other sibling maggots and eventually pupate successfully, more by chance, as each individual is as fit as the other on hatching and hence has equal probability of feeding and developing.

The tephritid, *B. dorsalis* is a polyphagous fruit-feeding maggot, but dominantly feeds on mango[2,3]. The adult females lay eggs below the rind of the mango using their piercing ovipositor. On hatching the maggots feed

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on the pulp, pass through three instars, and exit the fruit to pupate in the soil. Adults eclose after about a week. This is the typical life cycle of a fruit fly[2]. As the maggots are confined within the fruit in which they hatch, the onus to select the apt host and ensure a fit next generation rest solely with the adult females (mother). Therefore, it is hypothesized that a female mother will choose a fruit that has a higher biomass (pulp) that will suffice for the development of all the maggots that hatch from the eggs it can potentially lay at a point of time.

A second hypothesis is on the flip side; if the food is limiting, a female may limit its oviposition, or number of eggs laid in a fruit, proportional to the quantum of the resource, so that with lesser number of maggots intraspecific competition is avoided.

A third hypothesis can also be in place as a female may follow the *r* strategy[4], wherein it may first lay eggs like a 'machine' and a proportion of maggots develop to eclose into adults that survive to the next generation. So, the objective of the study was to examine if fruit biomass (pulp) quantum (measured as weight) influences the oviposition decision in the adult female tephritids, using three varieties of mango with differential weights.

The tephritid *B. dorsalis* was used for the present study and the host resource was mango fruits. The flies used were originally field-collected in 2007 from mango in Bangalore (12°58′N; 77°35′E), India, and maintained through several generations on banana as host[5] from August to May 2008, this also served to offset any learning experience on mangoes. The experiment was repeated on three varieties of mango, viz. *Alphonso*, *Banganpalli* and *Totapuri*.

Fruits of *Alphonso*, *Banganpalli* and *Totapuri* were selected from orchards maintained at the Indian Institute of Horticulture Research, Bangalore. An integrated pest management for fruit flies[6] was carried out in these orchards, and a cover spray three weeks prior to harvest was also given to ensure that the mangoes were free of infestation by *B. dorsalis*. The mangoes of the three varieties were randomly harvested at 80% maturity using manual harvesters which consisted of a stalk-snapper and a net-bag to gather the fruit without damage. Postharvest, disease-free and uniform-coloured (green) fruits were sorted and brought to the laboratory and heaped as a main lot, from which 80 fruits were again randomly selected for each variety. These fruits were washed and re-examined for any visible ovipositional punctures that could have occurred in the field. Fruits which were suspected to have any punctures were discarded, and replaced by random selection from the main lot. Thus 80 fruits were selected and numbered 1–80 using ballpoint refill pens, and their individual weights were recorded using a digital electronic balance with an accuracy of 0.01 g. The 80 fruits were then heaped and sub-divided into four quarters, of 20 fruits each. These fruits were introduced into four oviposition cages (60 × 60 × 60 cm)

@ 20 fruits/cage spaced with at least 2 cm between adjacent fruits, so that all fruits have equal exposure to flies. Each cage formed a set: to each cage 25 pairs of fruit flies (20-day-old), deprived of banana 24 h prior to the experiment but provided with water and yeast, were released. The fruits were removed from the oviposition cage 24 h after the introduction of the flies. The fruits thus exposed were taken out of the cage and the number of ovipositional punctures was counted using 10 × hand lens and were subjected to correlation analysis with fruit weight as an independent variable.

The data were also tabulated in the ascending order of fruit weight and further grouped into four weight classes for analysis of variance with respect to the number of oviposition punctures, with each class as treatment and each set as a replication. The coefficient *r* and LSD, both at $P = 0.05$ were the respective test criteria[7].

Post-ripening, each fruit was individually kept in a plastic container till the maggots pupated. The pupae were transferred to individual plastic containers with fine sand at the bottom (2 cm high), till the emergence of adults. The numbers of pupae, males and females (female : male ratio) were calculated and correlated with fruit weight, and the coefficient *r* at $P = 0.05$ was used as a test of significance. Among the varieties, sample number (*n*) was not uniform as some fruits rot beyond recovery.

The ranges of fruit weight and oviposition punctures in the varieties, viz. *Alphonso*, *Totapuri* and *Banganpalli* were 145–296 g and 1–160; 155–390 g and 1–101, and 196–431 g and 3–33 respectively. When the fruits were classified into four weight classes and subjected to ANOVA, it was found that the number of oviposition punctures did not show significant differences among the four weight classes irrespective of the weight of fruit, within a variety (Tables 1–3, Figure 1).

The mean number of oviposition punctures in the three varieties (Table 3) showed that the weight of the fruit had no significant correlation with the number of ovipositional punctures by the females, except in one out of the 16 sets (set two of *Alphonso*). This seems to be an exception as in the pooled analysis in all the varieties, the correlations between number of oviposition punctures and fruit weight were non-significant as also evident in the scatter plot (Figure 1).

In *Alphonso*, the mean pooled fruit weight was 197.38 g, with a mean number of oviposition punctures of 33.43. In *Totapuri*, the corresponding values were 244 g and 13.17 respectively, whereas in *Banganpalli* they were 273.18 g and 9.96 respectively (Table 3).

In this study we have considered the fresh fruit as the host resource and weight quantified the biomass of the resource. At the beginning of the study we hypothesized that with increase in fruit weight there will be a higher exploitation of food resource by the fruit fly to maximize its efficiency and fitness, in terms of more number of fit progenies to the next generation. The biology of the fruit

Table 1. Class intervals of experimental fruits on the basis of weights (g) for three varieties of mango

Weight group	*Alphonso* (g)	*Totapuri* (g)	*Banganpalli* (g)
T_1	145.0–170.0	155.0–208.0	196.0–245.0
T_2	170.1–192.0	208.1–245.0	245.1–263.0
T_3	192.1–222.0	245.1–294.0	263.1–288.0
T_4	> 222.1	> 294.1	> 288.1

Table 2. Number of oviposition punctures (mean/fruit)

Weight group	*Alphonso*					*Totapuri*				*Banganpalli*				
	I	II	III	IV	Pooled	I	II	III	Pooled	I	II	III	IV	Pooled
T_1	50.6	9.2b	24.2	12.4	25.75	8.4	4.8	7.8	8.65	6.2	6.0	7.4	10.6	10.3
T_2	33.0	9.6b	23.2	46.2	21.40	6.4	6.4	16.0	9.65	11.2	10.4	13.2	10.0	19.70
T_3	51.0	18.2	64.0	11.6	48.65	8.0	6.4	24.6	9.55	9.4	9.8	10	13.4	10.05
T_4	46.2	43.4	57.2	25.8	12.10	12.4	11.2	22.2	12.00	7.4	14.2	12.2	8.0	12.10
LSD ($P = 0.05$)	NS	22.5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS, Non-significant.

Table 3. Relationship between fruit size and fruit fly oviposition

Set	Fruit weight, mean ± S.D. (g)	No. of oviposition punctures, mean ± S.D.	$r*$ (between fruit weight and oviposition puncture)
Alphonso			
$n = 20$	200.92 ± 7.06	45.20 ± 6.57	0.037
$n = 20$	193.04 ± 6.88	20.10 ± 4.69	0.725
$n = 20$	211.93 ± 8.17	24.00 ± 7.91	0.088
$n = 20$	183.65 ± 6.28	44.45 ± 9.99	0.378
Pooled $n = 80$	197.38 ± 3.68	33.43 ± 3.91	0.186
Totapuri			
$n = 20$	277.77 ± 52.44	8.95 ± 1.68	0.291
$n = 20$	252.40 ± 57.15	7.20 ± 1.14	0.344
$n = 20$	214.33 ± 24.50	17.65 ± 4.94	0.338
$n = 10$	222.88 ± 10.40	24.6 ± 5.94	0.516
Pooled $n = 70$	244.00 ± 6.13	13.17 ± 1.86	0.027
Banganpalli			
$n = 20$	290.54 ± 9.65	8.55 ± 1.07	–0.031
$n = 20$	281.39 ± 11.27	10.1 ± 1.85	0.159
$n = 20$	278.00 ± 8.57	10.7 ± 1.77	0.334
$n = 20$	242.00 ± 6.05	10.5 ± 1.50	0.052
Pooled $n = 80$	273.18 ± 4.90	9.96 ± 0.78	0.104

*All *r* values are non-significant at $P = 0.05$.

fly, *B. dorsalis* is such that the adults use the fruit mainly to oviposit their eggs and the maggots that hatch, develop within the fruit in three instars, after which they exit and drop to the ground to pupate[8]. Though the maggots feed on the mango pulp, the choice of the host rests solely with the adult female mother, which oviposits and lays its eggs into the fruit pulp just below the rind. Generally, it is known that the choice of ovipositional sites is a stereotypic behaviour in many female insects that is conditioned by an innate capacity to select hosts which will satisfy the requirements of the subsequent developing larvae. Generally, phytophagous insects are known to be choosy about oviposition sites. To cite an example, the influence of fruit size on oviposition was studied in boll

weevil, *Anthonomous grandis grandis* Boheman on cotton[9]. Here the highest number of eggs was found in bolls between 5 and 8 mm diameter. Bigger bolls (> 10 mm) had lesser eggs, showing that the boll weevil had a nonrandom ovipositional strategy to maximize fitness.

In fruit flies, evidence of adaptive change in foraging behaviour from experience has been demonstrated in *B. dorsalis* and certain other tephritids[10]. Studies in a related tephritid fruit fly, *Ceratitis capitata* suggest the possibility of discriminative learning of size and colour. Though learning in *B. dorsalis* has not yet been recorded, exposure of the flies only to banana ruled out the influence of learning, if any, with respect to mango as it could vitiate the results of the present study.
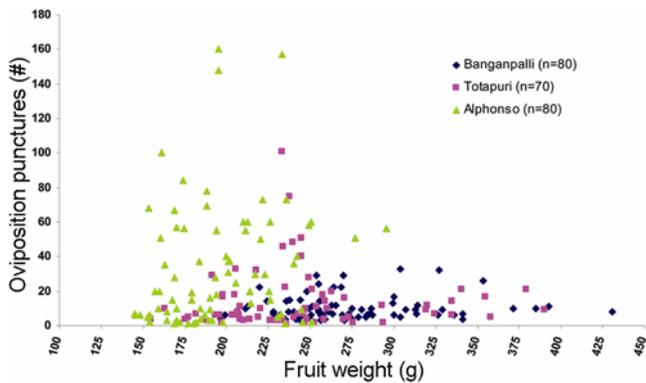
Figure 1. Scatter plot for fruit weight (g) and *B. dorsalis* oviposition punctures (#) in three mango varieties.

Theoretically, for a female fruit fly with multiple ovipositions on a single fruit, it is biologically advantageous to oviposit in a fruit with more pulp as more eggs can be laid for a unit of food resource (pulp) available to the maggots, spending lesser amount of time and energy. But this assumption was not true.

The objective of this study was to see whether fruit exploitation for oviposition varied with quantum (weight of fruit pulp). The results of the study indicate that in all the three varieties, oviposition by fruit flies was not influenced by the quantum (= weight) of the fruit pulp of mango. This does not exclude the role of other visual or olfactory cues. The plausible issue for a gravid polyphagous female seemed to be selecting a suitable host tree (mango) first and then to randomly oviposit within a host on an unlimited resource – fruits in this case, which on an average is 200–1000/mango tree, depending on the age of the orchard. So, we infer that fruit flies have a random selection of mango fruits for oviposition irrespective of fruit weight, either due to the incapability of discriminating a higher volume of visual or olfactory cues, expected in heavier fruits, or the fact that two 'small' fruits are as good as one 'big' fruit in a resource-unlimited situation, as in a typical mango orchard. So, for *B. dorsalis* to adapt a non-random ovipositional strategy once a host is selected does not confer any additional advantage. Thus, every fruit on a tree has equal probability of being selected by the fruit fly for oviposition. This was true for all three varieties chosen for the study and commercially speaking, every fruit is equally vulnerable to attack by fruit flies.

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The longest tusk of cf. *Anancus sivalensis* (Proboscidea, Mammalia) from the Tatrot Formation of the Siwaliks, Pakistan

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This communication reports the first discovery of a well-preserved tusk in the Siwaliks, which is assigned to species cf. *Anancus sivalensis*. The tusk, with a length of 271.8 cm (8 ft 11 in), was excavated from Late Pliocene sediments of Tatrot village (northern Pakistan), which are part of the Tatrot Formation of the Upper Siwaliks and range in age from 3.4 to 2.6 Ma. Such a long tusk is hitherto unknown from the

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